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# *PERIPLEURA* (ASTERACEAE: ASTEREAE): A NEW, AUSTRALIAN GENUS SEGREGATED FROM *VITTADINIA*

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## ABSTRACT

The nine species of *Vittadinia* subg. *Peripleura* (sensu Burbidge 1982) are completely distinct from the 20 species of subg. *Vittadinia*. Further, in their achenes with multinervate faces, the species of subg. *Vittadinia* are more similar to those of the Australian *Camptacra* and the New Guinean/Hawaiian *Tetramolopium* than they are to the species of subg. *Peripleura*, which have only a single pair of achenial nerves. Two-nerved achenes are found in other closely related Australian genera as well as related genera from South America. The distinctive tendency to produce multinervate achenial faces apparently is a specialization restricted to subg. *Vittadinia*, *Camptacra*, and *Tetramolopium*; and in the interpretation here, these three taxa are interrelated and occupy a phyletically advanced position relative to the species of subg. *Peripleura*. Accordingly, the latter are here segregated as the new genus **Peripleura** (Burbidge) Nesom, *stat. nov.*, with accompanying new combinations for species and varieties.

KEY WORDS: *Peripleura*, *Vittadinia*, Asteraceae, Astereae, Australia

In a taxonomic revision of the Australasian genus *Vittadinia* A. Rich., Burbidge (1982) recognized 29 species divided into two groups: subg. *Vittadinia* (20 species) and subg. *Peripleura* Burbidge (nine species). She also moved two species of Australian *Vittadinia* into the new genus *Camptacra* Burbidge, endemic to north-central and northeastern Australia (also see recent nomenclatural modification in *Camptacra* by Lander 1987a). The monotypic genus *Eurybiopsis* DC. (*Vittadinia* [*Eurybiopsis*] *macrorhiza* [DC.] A. Gray) was reinstated by Burbidge, but it has more recently been absorbed into *Minuria*

DC. (Lander & Barry 1980b; Lander 1987b). The present paper provides perspective on the taxonomy proposed by Burbidge regarding *Camptacra* and the two subgenera of *Vittadinia*.

The genera under discussion belong within a larger Australasian and South Pacific grouping that includes *Tetramolopium* Nees, a genus divided between New Guinea and the Hawaiian and Cook Islands and hypothesized by Lowrey (1986, p. 204) to be most closely related to *Camptacra* and *Vittadinia*, based on their common possession of "subulate style appendages, prominent barbellate pappus bristles, and several similar achene features." Additional genera of this group are *Ixiochlamys* Sond. and *Dichromochlamys* Dunlop (Dunlop 1980a, 1980b), *Minuria* DC., and the closely related *Kippistia* F. Muell. (Lander & Barry 1980a, 1980b), and *Iotasperma* Nesom (Nesom 1994).

Except for the disposition of *Eurybiopsis* as a synonym of *Minuria* and the exclusion of *Isoetopsis* Turcz., this group of essentially Australasian genera is the same as that delimited by Zhang & Bremer (1993) as the "*Vittadinia* group." The integrity of this group is accepted in a classification of the Astereae (Nesom in prep.), but at that broader level the *Vittadinia* group is hypothesized to further include the South American genera *Asteropsis* Less., *Blakiella* Cuatr., *Laennecia* Cass., *Microgynella* Grau, *Podocoma* Cass., and *Sommerfeltia* Less. (the "*Podocoma* group"). Morphologically, plants of the Australian *Vittadinia* group are characterized by the following: perennial (rarely annual) herbs or small shrubs with solitary heads on leafy (sometimes long-pedunculate) stems, the leaves and stems commonly glandular; (eglandular in *Minuria*, *Dimorphocoma*, and *Elachanthus*); disc flowers bisexual (with sterile ovaries in *Minuria*, a portion of *Tetramolopium*, *Dimorphocoma*, *Elachanthus*, and two species of *Ixiochlamys*), the corollas with short lobes and narrow tube longer than the limb; pistillate flowers numerous and in several series (1-seriate in *Dimorphocoma* and *Elachanthus*), with short, narrow, white to bluish ligules (yellow in *Kippistia*); achenes commonly with glandular surfaces (eglandular in *Minuria*), flat and 2-nerved (the faces multinervate in *Tetramolopium*, *Camptacra*, and *Vittadinia* subg. *Vittadinia*), with a tendency to produce a beak (*Ixiochlamys*) or neck (*Dichromochlamys*, *Vittadinia* subg. *Vittadinia*, somewhat less distinctly in *Minuria* and *Vittadinia* subg. *Peripleura*; pappus (1-) 2-3 series of basally persistent bristles (tardily caducous in *Vittadinia* subg. *Peripleura*); all chromosome counts have reported a number of $n=9$.

Burbidge distinguished *Camptacra* and the two subgenera of *Vittadinia* by contrasts in the following key (modified and extended from her original):

1. Achenes narrowly elliptic to elliptic-oblong, dark or purplish when mature, each face with 3 pairs of slender, slightly raised nerves, the pair of marginal nerves not thicker than those of the facial nerves; pappus 1-2-seriate. ..... *Camptacra*

1. Achenes mostly obovate to oblanceolate or cuneate, rarely uniformly pur-

plish though sometimes coloured on exposed parts, the faces with or without raised nervation, with a distinct pair of marginal nerves (except *V. pterochaeta* (Benth.) Black and *V. pustulata* Burbidge); pappus 1-3-seriate. .....(2)

2. Achenes with the seed in the upper portion, with a prominently narrowed, basal extension below the seed, with a dense basal tuft of appressed-ascending hairs, truncate at the apex to a broad pappus insertion (apex slightly narrowed and neck-like in *V. cervicularis* Burbidge, *V. megacephala* (Benth.) Black), the marginal nerves more or less at right angles to the apex; achenial faces with 3-5(-6) pairs of relatively slender, raised nerves, marginal nerves, conspicuously thickened, much broader than the facial nerves (marginal nerves not visible in *V. pterochaeta*; facial nerves usually not visible in *V. pterochaeta*, *V. pustulata*, and four others (see below); pappus 2-3-seriate, the bristles mostly equal the achene length or slightly longer, neither caducous not basally coherent. ..... ..... *Vittadinia* subg. *Vittadinia*

2. Achenes completely filled by the seed, lacking a narrowed, basal extension, without a basal tuft of hairs, abruptly rounded at the apex to the narrow insertion of the pappus, the marginal nerves usually apically confluent; achenial facial nerves absent, marginal nerves weakly or strongly thickened; pappus 1(-2)-seriate, the bristles mostly 1.5-2.5 times longer than the achene, often tardily caducous in groups minutely coherent at their bases. ..... ..... *Vittadinia* subg. *Peripleura*

The two subgenera of *Vittadinia*

The species of subg. *Peripleura* form a morphologically coherent group of closely similar species, most of them recently segregated from a broadly conceived *Vittadinia scabra* DC. by Burbidge (1982). The one other species already recognized at the beginning of Burbidge's study, *V. hispidula* F. Muell. *ex* A. Gray, was treated by Bentham (1866) as a synonym of *V. scabra*. There are no species of *Vittadinia* that could be interpreted as intermediate between subg. *Vittadinia* and subg. *Peripleura*. *Iotasperma* is the only Australian taxon besides subg. *Peripleura* with obovate, apically rounded achenes; among the South American genera closely related to the *Vittadinia* group, *Sommerfeltia* and *Laennecia* are particularly similar in achene morphology to subg. *Peripleura*.

The species of subg. *Vittadinia* constitute a presumably monophyletic group, based on the distinctively shaped achenes (with a sterile "foot" and truncate

apex) with a dense basal tuft of hairs and 2-3 seriate pappus that are characteristic of all species. Fourteen of these species produce achenes with consistent and conspicuous facial nervation (see Burbidge 1982, plates 3-9). Achenes of the remaining six species have mostly smooth faces (but see caveats below). Burbidge observed that the "species whose cypselas lack facial ribbing were probably derived from ribbed types. This view is based on characters visible in transverse section but it is consistent with the fact that ribbed-cypsela types have the widest geographical distribution" (1982, p. 5). Burbidge did not add any details regarding this observation, but it has been corroborated in the present study by dissecting achenes, removing the embryo, and studying the fruit walls mounted in Hoyer's solution.

The achenial morphology of subg. *Vittadinia* more closely resembles that of other Australasian genera than subg. *Peripleura*. Within the *Vittadinia* group, and including its close relatives in South America, achenes are strictly 2-nerved except in subg. *Vittadinia*, *Camptacra*, and *Tetramolopium*, where they have a number of slightly raised facial nerves in addition to the marginal pair. In these three taxa, however, only the marginal pair of nerves is vascularized; the facial nerves are essentially unvascularized fiber bundles, although a single element or group of tracheids may appear unpredictably and rarely in the fiber bundles, either near the achene base above the divergence of the lateral vascular bundles or toward the middle of the achene.

As noted by Burbidge (1982), the facial nerves in subg. *Vittadinia* arise at the achene base but commonly may not reach the apex; at least one of the *Vittadinia* species noted by Burbidge to lack facial ribbing, *V. megacephala*, sometimes may have such ribs externally visible in lower third of mature achenes. The same occurs in achenes of some *Tetramolopium* species, where facial nerves sometimes extend only a short distance above their basal origin. *Vittadinia pterochaeta* produces nearly terete achenes that are usually without any visible superficial ribbing (including even the lateral nerves), but numerous ribs are sometimes visible, particularly in immature achenes; the ribs are obscured by the heavily fibrous nature of the mature achene wall but their position can be seen more clearly in dissected and cleared material. In *V. pustulata*, the longitudinal ribbing is anastamosing rather than parallel, and the distinctive pustules that characterize the achene surfaces of this species are formed in the resulting interstitial spaces. In *Tetramolopium*, the facial nerves may be variable in number within species, populations, and even single heads, although "each taxon has a predominant number and configuration of nerves" (Lowrey 1986, p. 212).

Among genera outside of the *Vittadinia* group but potentially closely related to it (*e.g.*, within the *Brachycome* Cass. group, the *Grangea* Adans. group, and the *Conyza* L. group; Nesom in prep.), achenes are flat and 2-nerved, or if more nerves are present, most or all tend to be vascularized. The same is true for the genera of the South American *Podocoma* group, which is

closely related to the *Vittadinia* group. Achenes with numerous, essentially unvascularized facial nerves are an evolutionary specialization within the *Vittadinia* group, where they are characteristic of *Vittadinia* subg. *Vittadinia* but not of subg. *Peripleura*.

*Camptacra*

The species of *Camptacra* differ from those of subg. *Vittadinia* in their achenes without a basal extension or dense basal tuft of hairs. *Camptacra* differs from both subg. *Peripleura* and subg. *Vittadinia* in its achenes with relatively thin marginal nerves that are no thicker than the facial nerves (vs. marginal nerves strongly thickened in most of subg. *Peripleura* and some, but not all, species of subg. *Vittadinia*), embryos with a rounded base (vs. pointed base), and aspects of its disc corolla morphology. In *Camptacra*, the tube of the disc corollas is narrowly funnelform with the staminal filaments attached at or below the middle, with little or no swelling to indicate the position of attachment (vs. corolla tube narrowly cylindric with the staminal filaments attached near the middle or in the upper third, the position indicated by a slight swelling). *Camptacra* (as well as subg. *Peripleura*) differs from subg. *Vittadinia* in their reduced number of ray flowers and reduction in the number of pappus series.

*Tetramolopium*

*Tetramolopium* has received detailed taxonomic treatment, those of New Guinea by Koster (1966) and van Royen (1981), those of Hawaii in monographic detail by Lowrey (1986). The species are predominately woody shrubs of relatively high elevations, and they are geographically separated in New Guinea and smaller Pacific Islands from the main part of the *Vittadinia* group. Lowrey divided the genus into three sections: sect. *Tetramolopium* and sect. *Sandwicense* Lowrey are restricted to the Hawaiian Islands, except for *T. sylvae* Lowrey (sect. *Tetramolopium*), which also has been reported from the Cook Islands; sect. *Alpinum* Lowrey includes all of the New Guinean species and the Hawaiian *T. humile* (A. Gray) Hillebr.

Successful artificial hybridizations by Lowrey in all combinations among Hawaiian taxa of all three sections of *Tetramolopium* showed that genetic barriers are essentially lacking among these species (the New Guinean taxa have not been included in crossing experiments). There also are high genetic identities among the Hawaiian species, based on allozyme studies (Lowrey & Crawford 1985). In spite of this, there is considerable diversity within *Tetramolopium* in morphology and reproductive characteristics.

In *Tetramolopium* sect. *Alpinum*, the fertile achenes of New Guinean species usually produce a pair of mid-facial nerves, but the achenes of *T. humile* lack facial nerves or have a single pair present only near the achene base. Achenes in the rest of the genus have several nerves on each face in addition to the marginal nerves. The disc flowers in sect. *Tetramolopium* and New Guinean sect. *Alpinum* have consistently sterile ovaries; Koster (1966) noted that among the 21 New Guinean species treated by her, only *T. bicolor* Koster has fertile disc achenes, supplying a caveat that the apparent fertility might not be constant. *Tetramolopium humile*, however, has fertile ovaries, as do the species of sect. *Sandwicense*. The pappus in *Tetramolopium* is either 1- or 2-seriate.

The species of sect. *Sandwicense* stand apart from the others of the genus in their combination of bisexual, fully fertile disc flowers, heads in a corymboid-paniculate capitulescence (vs. solitary heads in other species of the genus), and shorter, relatively flat phyllaries with broad margins. If the genus is indeed monophyletic, and if the Hawaiian species are derived from New Guinean ones, as seems reasonable, one must make the unlikely but necessary hypothesis (as did Lowrey) that the species with a corymboid capitulescence and fertile disc ovaries have been derived from those with solitary heads and sterile ovaries.

Lowrey did not formulate a phyletic hypothesis for the species of *Tetramolopium*, nor did he include New Guinean species in his comparative genetic studies, but in view of the peculiar internal complexity of the genus, a phylogenetic investigation would be interesting, especially in a broader systematic context. Besides the species of sect. *Sandwicense*, there are no others in any genus of the *Vittadinia* group with a corymboid capitulescence, but there are such within *Olearia* Moench and related Australasian genera of subtribe Hinterhuberinae (Nesom 1993), which have other suggestive resemblances to these species of *Tetramolopium*.

## Other Australasian genera of the *Vittadinia* group

*Ixiochlamys*, *Dichromochlamys*, and *Iotasperma* produce necked or beaked achenes; the first two have markedly elaborated involucres. In *Minuria* and *Kippistia*, the disc flowers have consistently sterile ovaries and the pappus is 2-seriate, with the outer series much shorter than the inner. *Iotasperma* is specialized in its annual duration, reduced habit, and small, short-necked achenes with an essentially 1-seriate pappus. *Dimorphocoma* and *Elachanthus* both comprise eglandular, annual, few-headed herbs with a paucibracteate involucre, 1-seriate pistillate flowers, sterile disc ovaries, and scaly pappus. Among the taxa of the *Vittadinia* group in the Australasian region, *Camptacra* and the two subgenera of *Vittadinia* appear to be relatively unspecialized in most respects.

The foregoing discussion is summarized in the following observations: (1) the species of *Vittadinia* subg. *Peripleura* represent a morphologically distinct lineage not intergrading with subg. *Vittadinia*; (2) the degree of morphological separation between subg. *Peripleura* and subg. *Vittadinia* is roughly equivalent to that between *Camptacra* and subg. *Vittadinia*; and (3) the distinctively specialized, multinervate achenial faces produced by *Camptacra*, *Tetramolopium*, and subg. *Vittadinia* suggest that subg. *Peripleura* occupies a primitive evolutionary position relative to all three. If *Camptacra* is segregated as a genus, which appears to be justifiable, then subg. *Peripleura* should also be treated at generic rank. Burbidge observed that the nature of the relationship between the two subgenera of *Vittadinia* is obscure and noted (p. 17) that "If a narrow circumscription was adopted for genera of Astereae in Australia, [subg. *Peripleura*] could be regarded as distinct." In the view here, subg. *Peripleura* is no more narrowly circumscribed as a distinct genus than its close relatives, and the proposal is made below for its formal taxonomic elevation. The following key to the Australasian genera of the *Vittadinia* group provides additional perspective on the distinctions among these genera.

**Peripleura** (Burbidge) Nesom, *gen. et stat. nov.* BASIONYM: *Vittadinia* subg. *Peripleura* Burbidge, Brunonia 5:17. 1982. Type species: *Peripleura hispidula* (F. Muell. *ex* A. Gray) Nesom.

1. **Peripleura arida** (Burbidge) Nesom, *comb. nov.* BASIONYM: *Vittadinia arida* Burbidge, Brunonia 5:24. 1982.
2. **Peripleura bicolor** (Burbidge) Nesom, *comb. nov.* BASIONYM: *Vittadinia bicolor* Burbidge, Brunonia 5:25. 1982.
3. **Peripleura diffusa** (Burbidge) Nesom, *comb. nov.* BASIONYM: *Vittadinia diffusa* Burbidge, Brunonia 5:20. 1982.
4. **Peripleura hispidula** (F. Muell. *ex* A. Gray) Nesom, *comb. nov.* BASIONYM: *Vittadinia hispidula* F. Muell. *ex* A. Gray, Proc. Amer. Acad. Arts 5:118. 1862.
   a. *Peripleura hispidula* (F. Muell. *ex* A. Gray) Nesom var. *hispidula.*
   b. **Peripleura hispidula** (F. Muell. *ex* A. Gray) Nesom var. **setosa** (Burbidge) Nesom, *comb. nov.* BASIONYM: *Vittadinia hispidula* F. Muell. *ex* A. Gray var. *setosa* Burbidge, Brunonia 5:23. 1982.
5. **Peripleura obovata** (Burbidge) Nesom, *comb. nov.* BASIONYM: *Vittadinia obovata* Burbidge, Brunonia 5:25. 1982.
6. **Peripleura scabra** (DC.) Nesom, *comb. nov.* BASIONYM: *Vittadinia scabra* DC., *Prodr.* 5:281. 1836.

7. **Peripleura sericea** (Burbidge) Nesom, *comb. nov.* BASIONYM: *Vittadinia sericea* Burbidge, Brunonia 5:26. 1982.

8. **Peripleura spechtii** (Burbidge) Nesom, *comb. nov.* BASIONYM: *Vittadinia spechtii* Burbidge, Brunonia 5:19. 1982.

   a. **Peripleura spechtii** (Burbidge) Nesom var. **kimberleyensis** (Burbidge) Nesom, *comb. nov.* BASIONYM: *Vittadinia spechtii* Burbidge var. *kimberleyensis* Burbidge, Brunonia 5:20. 1982.

   b. *Peripleura spechtii* (Burbidge) Nesom var. *spechtii.*

9. **Peripleura virgata** (Burbidge) Nesom, *comb. nov.* BASIONYM: *Vittadinia virgata* Burbidge, Brunonia 5:21. 1982.

## KEY TO THE AUSTRALASIAN GENERA OF THE *VITTADINIA* GROUP (excluding Hawaiian *Tetramolopium*)

1. Achenes apically rounded or truncate, without a neck or beak. .....(5)

1. Achenes with a short neck or long beak. .....(2)

   2. Achenes with a long, filiform beak; receptacles flat or nearly so; involucres reflexed after fruiting. ..... *Ixiochlamys*

   2. Achenes with a short neck. .....(3)

3. Achenes with a prominently narrowed, basal extension below the seed, the basal extension densely tufted with stiff, appressed hairs. ..... ..... *Vittadinia* (in part)

3. Achenes without a narrowed, basal extension below the seed, the hairs at the base no denser than on the surface. .....(4)

   4. Achenes ca. 1 mm long, with a short, narrow neck; pappus bristles 1-seriate; involucral bracts never incurved. ..... *Iotasperma*

   4. Achenes ca. 2 mm long, with a short, broad neck; pappus bristles 2-seriate, the outer distinctly shorter than the inner; involucral bracts incurved after fruiting. ..... *Dichromochlamys*

5. Achenes with only a pair of lateral nerves, these variable in thickness, sometimes obscure or absent. .....(8)

5. Achenes usually with 2-numerous facial nerves between the pair of lateral nerves (facial nerves absent in six species of *Vittadinia*). .....(6)

6. Achenes with a prominently narrowed, basal extension below the seed, the basal extension densely tufted with stiff, appressed hairs. . ..... *Vittadinia* (in part)

6. Achenes narrowly oblong to obovate to oblanceolate, without a narrowed, basal extension below the seed, the hairs at achene base no denser than on the achene surface. .....(7)

7. Disc flowers with fertile ovaries; achenes usually with 3 pairs of facial nerves; herbs from a woody rootstock. ..... *Camptacra*

7. Disc flowers with sterile ovaries; fertile achenes with one pair of facial nerves, rarely none; woody-based shrubs or shrublets. . *Tetramolopium*

8. Achenes with a prominently narrowed, basal extension below the seed, the basal extension densely tufted with stiff, appressed hairs. . ..... *Vittadinia* (in part)

8. Achenes without a narrowed, basal extension below the seed, the hairs at achene base no denser than on the achene surface. ... (9)

9. Disc flowers with sterile achenes; pappus of ray and disc achenes different. . .....(10)

9. Disc flowers with fertile achenes; pappus of ray and disc achenes similar. . .....(12)

10. Disc flowers with 5 lobes; pappus of ray achenes of equal-length bristles, pappus of disc achenes of unequal bristles or of bristles and scales. ..... *Minuria*

10. Disc flowers with 3-4 lobes; pappus of ray achenes of scales or scales and bristles, pappus of disc (sterile) achenes of bristles. .....(11)

11. Leaves linear; ray achenes with pappus of scales. ..... *Elachanthus*

11. Leaves oblanceolate; ray achenes with pappus of scales and bristles. ... . ..... *Dimorphocoma*

12. Ray flowers with yellow corollas, the ovaries often sterile; disc flowers 4-merous; achenes apically truncate, with a corresponding broad pappus insertion. ..... *Kippistia*

12. Ray flowers with white to bluish corollas, the ovaries fertile; disc flowers 5-merous; achenes apically rounded to a narrow pappus insertion. ..... *Peripleura*

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## LITERATURE CITED

Bentham, G. 1866. *Vittadinia. Flora Australiensis* 3:489-492. Lovell Reeve and Co., London, Great Britain.

Burbidge, N. 1982. A revision of the *Vittadinia* A. Rich. (Compositae) together with reinstatement of *Eurybiopsis* DC. and description of a new genus, *Camptacra.* Brunonia 5:1-72.

Dunlop, C.R. 1980a. *Dichromochlamys*, a new genus in Asteraceae (Astereae). J. Adelaide Bot. Gard. 24:235-239.

_____. 1980b. A revision of *Ixiochlamys* (Asteraceae: Astereae). J. Adelaide Bot. Gard. 24:241-252.

Koster, J.T. 1966. The Compositae of New Guinea I. Nova Guinea 24:524-612.

Lander, N.S. 1987a. New combinations in *Camptacra* N. Burb. (Asteraceae: Astereae). Nuytsia 6:61.

_____. 1987b. New combinations in *Minuria* DC. (Asteraceae: Astereae). Nuytsia 6:63-66.

Lander, N.S. & R. Barry. 1980a. Reinstatement of the genus *Kippistia* F. Muell. (Asteraceae, Astereae). Nuytsia 3:215-219.

_____. 1980b. A review of the genus *Minuria* DC. (Asteraceae, Astereae). Nuytsia 3:221-237.

Lowrey, T.K. 1986. A biosystematic revision of Hawaiian *Tetramolopium* (Compositae - Astereae). Allertonia 4:204-264.

Lowrey, T.K. & D.J. Crawford. 1985. Allozyme divergence and evolution in *Tetramolopium* (Compositae: Astereae) on the Hawaiian Islands. Syst. Bot. 10:64-72.

Nesom, G.L. 1993. *Aztecaster* (Asteraceae: Astereae), a new ditypic genus of dioecious shrubs from México with redefinitions of the subtribes Hinterhuberinae and Baccharidinae. Phytologia 75:55-73.

_____. 1994. Taxonomic dispersal of Australian *Erigeron* (Asteraceae: Astereae). Phytologia 76:143-159.

Royen, P. Van. 1981. *Alpine Flora of New Guinea* (Vol. 2). J. Cramer, Vaduz, Liechtenstein.

Zhang, X. & K. Bremer. 1993. A cladistic analysis of the tribe Astereae (Asteraceae) with notes on their evolution and subtribal classification. Pl. Syst. Evol. 184:259-283.